



SHILAP Revista de Lepidopterología

ISSN: 0300-5267

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Sociedad Hispano-Luso-Americana de  
Lepidopterología  
España

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some studies on Saturniidae (Lepidoptera: Saturniidae)

SHILAP Revista de Lepidopterología, vol. 34, núm. 133, 2006, pp. 5-12

Sociedad Hispano-Luso-Americana de Lepidopterología  
Madrid, España

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# Phylogenetic hypothesis and classification: theoretical and methodological issues with reference to some studies on Saturniidae (Lepidoptera: Saturniidae)

L. Racheli & T. Racheli

## Abstract

Some theoretical and methodological issues on both phylogenetic hypothesis and classification are discussed in the light of some recent papers on Saturniidae. In particular, the use of molecular data in systematics of Saturniidae is discussed, and the recent phylogeny of "Bunaeinae" and the recognition of the Urotini are debated. Alternatively, our comments are criticisms or clarifications regarding different views discussed in the papers taken into consideration. The aim of this paper is to open a discussion forum on the arguments debated below.

KEY WORDS: Lepidoptera, Saturniidae, Phylogenetic hypothesis, classification.

## Hipótesis filogenética y clasificación: salidas teóricas y metodológicas con referencia a algunos estudios sobre Saturniidae (Lepidoptera: Saturniidae)

## Resumen

Se discuten algunas salidas teóricas y metodológicas sobre ambas hipótesis filogenéticas y clasificación en base a la luz de los recientes trabajos sobre Saturniidae. En particular, se discute el uso molecular en la sistemática de los Saturniidae, y se debate la reciente filogenia de "Bunaeinae" y el reconocimiento de los Urotini. Alternativamente, nuestros comentarios son críticas o clarificaciones con respecto a diversas opiniones discutidas en los trabajos considerados. El ánimo de este trabajo es abrir un forum de discusión sobre los argumentos debatidos debajo.

PALABRAS CLAVE: Lepidoptera, Saturniidae, Hipótesis filogenética, clasificación.

## Introduction

This paper discusses a range of problems and implications concerning the application of methods in phylogenetic reconstructions, the related hypotheses and the explanations versus speculations which are deduced from them. These issues are discussed in relation to some recent attempts of classification certain lineages of Saturniidae which are rearranged in the absence of rigorous phylogenetic hypotheses or on the basis of theoretical and methodological misunderstandings. Other papers are simply used as examples in discussing the flawed but widely used criterion of arrangement-based on subjective speculations, hence unscientific conjectures. Given that biological classifications are usually arranged according to one of the three major schools recognized (i. e. evolutionary taxonomy, phylogenetic (or cladistic) taxonomy and phenetic taxonomy, see e. g. SCHUH, 2000), our comments are explained against the background of these three different approaches. Although these three schools differ in their theoretical underpinnings, this difference is often not clear in some of the statements in the articles here considered.

Our comments under the three headings below regard a series of different arguments. Comments on

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two of the few published phylogenetic hypotheses for Saturniidae lineages (those by BALCÁZAR & WOLFE, 1997 and by REGIER *et al.*, 2002) concern clarifications about questionable choices made by the authors. Criticisms of doubtful arrangements recently introduced by COOPER (2002), in particular his phylogeny of “Bunaeinae”, deals with the author’s basic misunderstanding of phylogenetic principles in compiling his data matrix.

A further disappointment regards a justification used by BOUYER *et al.* (2004) in their criticism to one of the COOPER’s (2002) arrangements. Indirectly, their arguments confirm that an inductive arbitrary-based approach is flawed and it is an unsuggestable criterion to present a classification. Against this conceptual premise, the conclusion by BOUYER *et al.* (2004) does not differ from that of COOPER (2002) for the reason that they are aware of the absence of evidence but they support an analogous arrangement namely the reappraisal by OBERPRIELER (1997) of the typological classification of BOUVIER (1936).

Although we disagree in different ways with other authors in the terms discussed below, our main aim is to open a debate that will improve our knowledge not only on Saturniidae but also on the theoretical and methodological issues treated here. Criticisms or simply clarifications are welcome, and critical discussion in a discussion forum with opponents is a suitable and productive way of advancing the general understanding and appreciation of the issues we raise.

Concluding this brief premise, we quote a question from the article on taxonomy by VANE-WRIGHT (2003): “Can taxonomy continue to be a game in which anyone can play?”. At least regarding the publications by D’ABRERA (1998) and that by COOPER (2002), our reply is negative as it will be debated below.

#### Comments on some recent studies on Saturniidae and the use and abuse of molecules in phylogenetic reconstructions

Recent attempts by BALCÁZAR & WOLFE (1997) and REGIER *et al.* (2002) aimed at introducing phylogenetic hypotheses to elucidate relationships among Saturniidae taxa, reveal some problems. For instance, it is unclear why BALCÁZAR & WOLFE (1997) used contradictory methods (phenetic and parsimony-based methods) to present their hypotheses for Ceratocampinae. The use of contradictory methods (phenetic and parsimony-based) is neither a test nor a comparison, and no useful information can be gained from comparing them. In the literature, there are many examples of applications of contradictory phylogenetic methods (e. g. maximum parsimony, maximum likelihood and Bayesian inference) but this is not a justification. Indeed, it means only that many researchers did not discern theoretical differences among these methods. The hypotheses obtained by these three methods have totally different informative power, and maximum parsimony provides the most severely tested hypotheses, i. e., those that have the greatest explanatory power (FARRIS, 1983; KLUGE, 1997, 2001).

In the second example, REGIER *et al.* (2002) seem to confer absolute importance to the bootstrapping values obtained, as clearly stated in their chapter “Results and discussion” (see pp. 16-20). Firstly, the bootstrapping support is not itself an absolute measure of significance but a method of data exploration. Also, high bootstrap values do not in themselves mean a well supported hypothesis of relationships. Although this resampling technique is widely used in the majority of the phylogenetic analyses presented, its usefulness remains very questionable (KLUGE & WOLFE, 1993; GRANT & KLUGE, 2003). A proponent of this technique (BROWN, 1994) affirms that its use in “phylogeny estimations lacks rigorous justification”. Usually, proponents of these methods (e. g., bootstrapping) give an absolute significance to the high values of the measure of support. They judge a high value in terms of an accurate result. Is this the aim of a phylogenetic analysis? Is a hypothesis really judged by a statistical measure of support? As pointed out elsewhere (RACHELI, 2004), we view phylogenetic systematics according to the arguments outlined by KLUGE (1998).

Secondly, REGIER *et al.* (2002 contra NÄSSIG, 1991 and OBERPRIELER & NÄSSIG, 1994) suggested to return *Saturnia isabelae* (Graells, 1849) to its former genus *Graellsia* Grote, 1896 according to the results obtained. However, this conclusion is based on a consensus tree which is inferred from a molecular data matrix only. No total evidence analysis has been presented, and their statement remains arbitrary and questionable. We are not discussing whether *isabelae* must be or must not be included in *Actias* Leach,

1815 but only that systematic and taxonomic arrangements must be based on total evidence analysis, and never on a consensus tree (BARRETT *et al.*, 1991). The most valuable statement is that evidence based on two nuclear genes supports a differentiation among *isabelae* and the other *Actias* (sensu lato), but is this topology confirmed in all the most parsimonious trees obtained? This is not clearly outlined. Furthermore, REGIER *et al.* (2002) mainly based their results on maximum likelihood tree/s. Although they presented also maximum parsimony analyses of their data matrices, they did not indicate whether *isabelae* is a paraphyletic taxon in respect to *Actias* (sensu lato) in the maximum parsimony trees obtained. In brief, the systematic and taxonomic position of *isabelae* is an open debate in the light of this new evidence and in the consideration of the previous arrangements, however, not based on phylogenetic hypotheses.

To explain in details our view, we report the recent case of the Nymphalid genus *Inachis* Hübner, 1819. Since a long time the validity of this genus has not been questioned. A recent total evidence analysis by WAHLBERG & NYLIN (2003) evidenced that *Inachis* should be treated as a synonym of *Aglais* Dalman, 1816. Because that analysis has been based on all the available evidence (morphology + ecology + behaviour + molecules), their results objectively supported that *Inachis* is a synonym of *Aglais*. In this specific example, there are no arguments against this new arrangement in the light of all available evidence used in that analysis.

According to the above reasoning which treats the cases of *Graellsia* and *Actias*, that of *Inachis*, and the use of total evidence approach, the result of a recent phylogenetic analysis conducted by YLLA *et al.*, (2005) indirectly replies to part of the above questions. Unfortunately, their analysis arrived in our hands when our manuscript was already submitted to the editor. However, their analysis evidenced a basal position of *Graellsia* in respect to the other *Actias* (s. l.) which supports the arrangement in a separate genus for *Graellsia*.

According to the above example, we briefly discuss the use and abuse of molecules in phylogenetic reconstructions. The rapid increase of phylogenetic hypotheses of various organisms based on molecular characters are not viewed as a further contribution to improve the scientific knowledge but like an absolute truth paradoxically. Previous hypotheses for the same taxa but based on morphological characters are discarded in favour of these new hypotheses. Undoubtedly, new evidence based on molecular characters is a valuable tool to explain evolutionary relationships among organisms but hypotheses based on molecules cannot be viewed a priori as more informative than the others. A second point regards the use of molecules in phylogenetic reconstructions. The “war” among categories of evidence in phylogenetic systematics is not accepted and the artifacts (namely morphology vs. molecules and morphology and molecules) must be discarded in favour of analysis based on molecules + morphology + all other kinds of available evidence according to the principle of total evidence (sensu KLUGE, 1989). Indeed, there are no categories of evidence in nature (NIXON & CARPENTER, 1996).

Although the divide et impera strategy has been a valuable tool during Romans’ times, the proponents of separate analysis (namely taxonomic congruence and/or supertree approach) have failed in their approach to phylogenetic systematics (see KLUGE & WOLF, 1993; NIXON & CARPENTER, 1996; GRANT & KLUGE, 2003).

#### The COOPER’s (2002) phylogeny of “Bunaeinae”

There are several criticisms which can be addressed to the attempt to present a phylogeny of “Bunaeinae” made by COOPER (2002), but only some of them are here discussed with special reference to some theoretical inaccuracies. Firstly, he never clarified according to which grouping methods his phylogeny has been performed. Even if he generically argued about some shared features among the taxa analyzed, in some cases characters (or groups of them!; e. g. characters n. 2, 6, 14 and many others) were used in supporting some terminal taxa rather than synapomorphies to recognize monophyletic groups. Several monophyletic groups are supported only by redundant characters whereas the monophyly of other lineages is hypothesized only by state-transformations of the same character used in different contradictory ways. Paradoxically this is a secondary problem. Clearly, it is possible to discuss in detail each character selected in compiling his data matrix but a basic misinterpretation made by COOPER (2002) conditioned a priori his phylogenetic analy-

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sis. The use of a character such as the presence of the ocellus in the forewing cannot be coded as a multistate character with other independent characters such as antennae bipectinate or ground colour of the wing. Then, COOPER (2002) misinterpreted the use of characters in his phylogenetic reconstruction and he failed to recognize the intrinsic value of character independence. This misunderstanding about the character independence is sufficient for discarding his phylogenetic analysis without further comments.

A different problem regards the arrangements proposed by COOPER (2002) which are not based on his "phylogenetic hypothesis". Indeed, it seems that these arrangements are raised ad hoc to elucidate relationships among the taxa analyzed, otherwise unresolved. Introducing these arrangements, COOPER (2002) does not give a detailed description supporting his decisions and for this reason it is difficult to understand some of his choices. For instance, he described the genus *Oberprieleria* and argued that its sister taxon is *Melanocera* but this statement is not evidenced in his phylogeny of "Bunaeinae". There are so many inconsistent arguments and incongruences comparing his hypothesis and his conclusions that it is very difficult to understand the value of this contribution. Lastly, it is not by chance that a review and some preliminary comments by BOUYER (2004) and NAUMANN (2004) agree with our opinion.

#### A justification rejects the tribe "Tagoropsini" but is the tribe Urotini "better" than the former?

Describing the preimaginal instars of *Pseudantheraea discrepans* (Butler, 1878), BOUYER *et al.* (2004) critically commented the inclusion of four genera (*Tagaropsis* Felder, 1874, *Maltagorea* Bouyer, 1993, *Pseudantheraea* Weymer, 1892 and *Sinobirma* Bryk, 1944) into a new tribe "Tagoropsini" introduced by COOPER (2002). These genera were previously assigned to the tribe Urotini although this arrangement needs still confirmation (OBERPRIELER, 1997; BOUYER *et al.*, 2004).

We generically agree with the arguments debated by BOUYER *et al.* (2004) about the inappropriate arrangement proposed by COOPER (2002) but in support of their statement, they claimed that they do not follow it because it "is not based on any solid phylogenetic argumentation". This statement seems an unsound justification because most of the current systematic and taxonomic arrangements of the Worldwide Saturniidae are not consolidated on phylogenetic analysis. For example and among others, the linear classification of the New World Saturniidae is arranged according to the "classical evolutionary taxonomists" classifications (see e. g., MICHENER 1952; LEMAIRE, 1996 for a synthesis of his revisions) but both are not based on phylogenetic reconstructions hence these classifications remain unsound and questionable. However, this is an old problem related to the "classical evolutionary taxonomists" classification which is based on the absence of a logical criterion but mainly on an explicit and defensible methodology (HENNIG, 1975 *contra* MAYR, 1974; PLATNICK, 1978 *contra* BOCK, 1978; MAYR & BOCK, 2002 but see WILEY, 1975 and FARRIS, 1979). Historically, the taxonomic arrangements - here, we mainly refer to the lowest categories namely tribe, genus, subgenus, "group", "subgroup", species. However, substantial differences also occur in highest categories as summarized by REGIER *et al.* (2002: fig. 1) and ROUGERIE (2005) - are mainly based on personal interpretations more than on hypothesis, evidence and explanation. For this reason when the arrangement of a given taxon is not supported by evidence (due to the lack of data or for the objective complexity of the taxon/a under study), the arrangement itself is usually established on the basis of inductive speculations.

The cladistic hypothesis of the Ceratocampinae (see BALCÁZAR & WOLFE, 1997: figs. 69-70) resulted in a basal position of *Neorcardia* Draudt, 1930 to the remaining Ceratocampinae. This result gives the opportunity to raise a tribal status for *Neorcardia* on the basis of the hypothesis obtained. We do not take into consideration that the analysis yielded 22 most parsimonious trees and obviously we assume that this topology has been obtained in all the most parsimonious trees. Although this arrangement has never been proposed, no criticisms can be addressed to this hypothetical arrangement because that hypothesis must be viewed in the light of the evidence used at that time in compiling their data matrix. It is obvious that further evidence could discard such hypothesis. This hypothetical arrangement is the most suitable way to perform a classification of Saturniidae according to the Hennigian view of phylogenetic systematics and the formal classification. This arrangement is most suitable not because it is more stable but only because it mirrors a phylogenetic hypothesis (i. e., a systematization of taxa according to their hierarchical and natural

relationships) obtained through the application of maximum parsimony. An hypothesis obtained through a total evidence analysis using the maximum parsimony criterion has the greatest explanatory power (GRANT & KLUGE, 2003).

Regarding the stability, the title of the chapter by GAFFNEY (1979) - who indirectly replies also to MAYR & BOCK (2002: 189-190) and KRAUS (2004) - "Classification: stability is ignorance" and the related arguments explained in that paper, mirror our ideas about a classification based on a phylogenetic hypothesis where the stability has been shown as undesirable. Although the stability has been used as a criterion in supporting an approach against the others, it is conceptually flawed because each hypothesis can maintain or modify the preceding one according to the logic of progressive research programme (see e.g. DOMINGUEZ & WHEELER, 1997; KLUGE, 2005: 20-21).

In contrast, the unsound alternative arrangement allows to use any kind of speculations in support of personal but unscientific taxonomic arrangements. The example regarding two of the arguments just discussed above (the taxonomic arrangement and the case of *isabelae*) confirms our critical view about this kind of "handmade" taxonomy. The re-arrangement of *Graellsia* at generic status (D'ABRERA, 1998 *contra* NÄSSIG, 1991) is based on spurious statements, such as its restricted distribution to SW Europe.

Given the uselessness of the new arrangement introduced by COOPER (2002) in the light of the present knowledge and however in absence of a bold hypothesis, the current classification and the validity of the same tribe Urotini remain questionable, as also admitted by OBERPRIELER (1997) and BOUYER *et al.* (2004). In this context, why Urotini is a plausible arrangement and "Tagoropsini" is not? It is our opinion that we cannot explain and support the arrangements according to ad hoc explanations or to unsound justifications based on intuitive arguments supporting an arrangement against another arrangement. If a hypothetical classification of Saturniidae is mostly based on intuitive arguments, it seems obvious that it will be always subjected to unobjective interpretations and it will never be based on hypothesis, evidence and explanation. The current knowledge about these taxa (*Sinobirma*, *Tagaropsis*, *Maltagorea* and *Pseudantheraea*) and related genera, tentatively arranged into Urotini, reveals only that evidence supports a monophyletic group which includes *Sinobirma*, *Tagaropsis*, *Maltagorea* and *Pseudantheraea*. The phylogenetic relationships of this group with other taxa and the inclusion of further taxa in the supposed tribe Urotini remain an unresolved question (e. g. OBERPRIELER, 1997 but see ROUGERIE, 2005). BOUYER *et al.* (2004) supported this point but failed to explain their choice in support to one of the two arrangements.

Undoubtedly, the attempt at presenting a revised classification of Afrotropical Saturniidae by OBERPRIELER (1997) is praiseworthy but he made some contradictory choices in particular regarding Urotini. In his introduction, OBERPRIELER (1997) argued about the necessity of a phylogenetic-based classification of Saturniidae which mirrors hierarchical and natural assemblages. Indeed, his paper deals with a synthesis of information regarding characters mainly based on preimaginal stages (see also OBERPRIELER & NÄSSIG, 1994), and a re-assessment of the typological Urotini originally proposed by BOUVIER (1936). Although OBERPRIELER (1997) admitted the absence of evidence in support of this arrangement, the tribe Urotini is an artificial and not a natural group, and it seems more a group of incertae sedis. By implication, the recognition of the five major groups of Afrotropical Saturniidae by OBERPRIELER (1997) is objectively a classification in the light of the characters selected by OBERPRIELER & NÄSSIG (1994). Perhaps, it is not by chance alone that REGIER *et al.* (2002), NAUMANN (2004) and ROUGERIE (2005) report and use the classification of OBERPRIELER (1997).

Lastly, the Urotini includes at least three main monophyletic groups with the genera *Sinobirma*, *Tagaropsis*, *Maltagorea* and *Pseudantheraea* which form one of the monophyletic groups according to the evidence recently summarized by ROUGERIE (2003). Paradoxically, the data summarized by ROUGERIE (2003) and, more importantly, the recent total evidence analysis presented by ROUGERIE (2005) support a different taxonomic rank for this monophyletic group which is in agreement to the recognition of the tribe "Tagoropsini" proposed by COOPER (2002).

## Epilogue

Two main points of the above discussion are herewith summarized. These are not criticisms to the pa-



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pers of BALCÁZAR & WOLFE (1997), BOUYER *et al.* (2004) or to that of REGIER *et al.* (2002) but eventually they are clarifications about our position with comments to the several problematic issues regarding the current classification of Saturniidae. We are proponents of studies, such those presented by BALCÁZAR & WOLFE (1997) and REGIER *et al.* (2002), but the evaluation of methodologies play a fundamental role in the formulation of hypotheses, explanations and arrangements accordingly. Our opinion is that unsound speculations, new arrangements on hypotheses obtained on partitions of data matrix or ad hoc explanations are not the proper ways to present a classification of Saturniidae or whatever classification. The unscientific “better than nothing” claim cannot be used as a justification for the current classification of this family or for alternative but questionable attempts (e. g. COOPER, 2002). Besides the phylogenetic hypotheses discussed above, only few further examples have been presented (e. g. PEIGLER, 1989; 1993) and the potential analyses to explain relationships among and within most of the Saturniid lineages can be achieved only in many years and through several studies. The goal of the present clarification is to underline some theoretical and methodological differences among methods aimed at obtaining a classification of Saturniidae which discards the arbitrary-based statements and the ad hoc explanations as fundamental tools in systematics and taxonomy.

Concluding, we are not advocating the adoption of the Phylogenetic nomenclature (*sensu* PLEIJEL & ROUSE, 2003; LAURIN & CANTINO, 2004) but when differences among these competing but alternative taxonomic methods will be clarified (at present there are controversial debates and different positions on this issue, see e. g. NIXON & CARPENTER, 2000; NIXON *et al.*, 2003; KLUGE, 2005; PLEIJEL & ROUSE, 2003), the use of one of them will be necessary. Objectively, it will be due to the evaluation of these approaches in the light of the Lakatosian context of research programmes (LAKATOS, 1970), where competing methods really and definitely reveal their soundness. In any case, the taxonomic arrangements based on linear classification are merely anachronistic.

If the proposed discussion forum is going to see the light then the hole where to put the seed for a Saturniid “tree” will be dug out.

### Acknowledgements

In the literature, there are many examples of studies, on both animal and plant organisms, which are questionable for different reasons but our choice to examine only some articles on Saturniidae was due only to our interest about this taxon. A preliminary draft of the present paper has been sent to specialists and amateurs dealing with Saturniids, but only few of them improved the text with their suggestions. Our thanks are due to Ric Peigler and Alberto Zilli for their comments. Roberto Vinciguerra discussed parts of an early version with the senior author. Unnecessarily they shared our opinions and it is obvious that their suggestions were accepted or rejected according to our views. Rodolphe Rougerie gives several constructive comments on our manuscript. Most of his comments have been not included in this version because we hope in his reply through a further paper which will be the first step to open the suggested forum. Wolfgang A. Nässig and an anonymous reviewer gave comments and criticisms. Regarding the suggestions of the reviewer, we found some constructive criticisms but also many requests of explanation about phylogenetic methods (properties and differences among them), and regarding some concepts (e. g. informative power, available evidence, and others) used in the text. All these arguments are not the aim of the present paper. Finally, Ric Peigler, Rodolphe Rougerie and Ulrich Brosch kindly sent papers of literature.

A particular thank is due to the late Clas M. Naumann for his early application of the Hennigian view of phylogenetic systematics to a lepidopteran lineage (Sesiidae) but also for the several occasions spent with us in discussing numerous issues of comparative biology. We are convinced that Clas should have been amused and interested at reviewing the present paper which is dedicated to him.

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(Recibido para publicación / Received for publication 10-X-2005)  
(Revisado y aceptado / Revised and accepted 1-XI-2005)